Z. Säugetierkunde 55 (1990) 11–15

ISSN 0044-3468

Hyoid-dentary articulations in golden moles (Mammalia: Insectivora; Chrysochloridae)

By G. Bronner, Elizabeth Jones and D. J. Coetzer

Department of Mammals, Transvaal Museum, and Department of Anatomy, University of Pretoria, Pretoria, South Africa

Receipt of Ms. 14. 4. 1988

Abstract

Studied the general structure, topography and possible functions of the hyoid region in nine golden mole species. Unusual in-situ articulations between the enlarged stylohyal bones, and the dentaries, were found in all specimens examined. Osteological evidence suggests that hyoid-dentary articulation is an unique anatomical feature characteristic of all chrysochlorids. Its apparent functions are to enhance manipulatory action of, and support for, the tongue during prey handling and mastication, but this remains to be confirmed.

Introduction

Hyoid-mandible articulations occur in some osteichthyian fishes (de Beer 1937; Hildebrand 1974), but have never been recorded in higher vertebrates. Improved museum preservation techniques recently enabled us to detect conspicuous articulation between the large stylohyal bone and the dentary in the Hottentot golden mole *Amblysomus hottentotus* (A. Smith, 1829). Further investigation revealed that hyoid-dentary articulation (Fig. 1) in situ is an unique characteristic of all chrysochlorids. In this preliminary note,

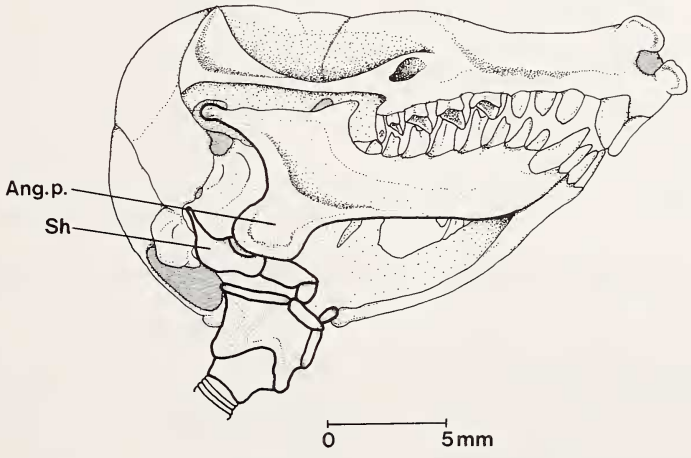

Fig. 1. Skull and hyoid region of an *Amblysomus julianae* Meester, 1972 (TM 39932) showing the articulation between the enlarged stylohyal bone (Sh) and the angular process (Ang. p.) of the dentary

the general structure and possible functions of the hyoid apparati in golden moles are briefly considered.

Golden moles are small, solitary, subterrestrial eutherians about which little is known. Of the 18 species (representing seven genera) endemic to sub-Saharan Africa, 15 are

restricted to southern Africa (Meester 1974; Meester et al. 1986). Morphologically and ecologically, they show marked convergence with the true moles (Talpidae), and especially the marsupial "mole" *(Notoryctes typhlops)* of Australia (Kuyper 1985; Nevo 1979). Taxonomically, the Chrysochloridae were traditionally associated with the tenrecs (Tenrecidae) of Madagascar (Butler 1956). However, there is no unequivocal evidence favouring a close taxonomic relationship between these families (Butler 1972), and chrysochlorids possess so many unique anatomical features that Broom (1915, 1916), Bugge (1974) and Roux (1947), amongst others, suggested that they should be assigned to a distinct order (the Chrysochloridea).

Materials and methods

Dobson (1882) und Sprague (1944) found that the hyoid apparati of golden moles have an unusual, specialized structure, and while the former author noted a large, concave surface on the anterior aspect of the stylohyal bone, he described this as a site of hyoid-tympanic bulla junction. However, examination of preserved specimens representing eight species (see Table), suggested to us that the anterior surface of the stylohyal articulates not with the auditory bulla, but with the base of the dentary. This was subsequently confirmed by: examination of intact, double-stained *Chrysochloris asiatica* showing the hyoid bones in situ; X-ray photography of five species (*A. hottentotus* – TM 39 201; *A. iris* – TM 29 313; *Chrysochloris asiatica; Chrysospalax trevelyani* – TM 30 262; *Eremitalpa granti* – TM 39 261); and dissection of four *A. hottentotus* (TM 39 200; TM 39 201; TM 39 202; TM 39 205) and one *A. iris* (TM 39 204).

Results and discussion

The hyoid apparati of all species examined, while differing markedly in size, are morphologically similar. Each comprises five pairs of ossified segments that form a chain linking the larynx with the cranium and dentaries (Fig. 2). The basihyal (which is proximal in this discussion) is a small, transverse bar (of paired origin; de Beer 1937) that meets distally with the thyrohyals and hyoid cornua. The long, cylindrical thyrohyals run caudolaterally from the basihyal to join the thyroid cartilage via the chondrohyoid cartilages (which are partly ossified). Each anterior hyoid cornu consists of three bony elements (a condition Howes 1896 termed "integrocornuate"), which in proximal-distal order are: 1. a small, squat ceratohyal that runs rostromedially; 2. a short, rectangular or triangular epihyal that is deflected laterally; 3. a robust, bulbous stylohyal with a tapering distal extremity (the styloid process) which projects rostrodorsally to join with the tympanic bulla via a long, slender tympanohyoid cartilage. As in most other insectivores,

Table 1. **Chrysochlorid specimens in the Transvaal Museum (TM) examined during the study**

Species	TM accession numbers
Chrysospalax trevelyani (Gunther, 1875)	39438, 39927
Chrysochloris asiatica (Linnaeus, 1758)	39235, 39237, 39238, 39239, 39245, 39291, 39293, 39294, 39295
Eremitalpa granti (Broom, 1907)	39261
Chlorotalpa duthiae (Broom, 1907)	39456
Chlorotalpa sclateri (Broom 1907)	39439, 39442, 39445
Calcochloris obtusirostris (Peters, 1851)	39470
Amblysomus iris Thomas & Schwann, 1905	39164, 39165, 39167–39173, 39175, 39176, 39204, 39933
Amblysomus hottentotus (A. Smith, 1829)	39200–39203, 39205, 39206, 39240, 39246–39248, 39260, 39296, 39297, 39422, 39423
Amblysomus julianae Meester, 1972	39769, 39770, 39932

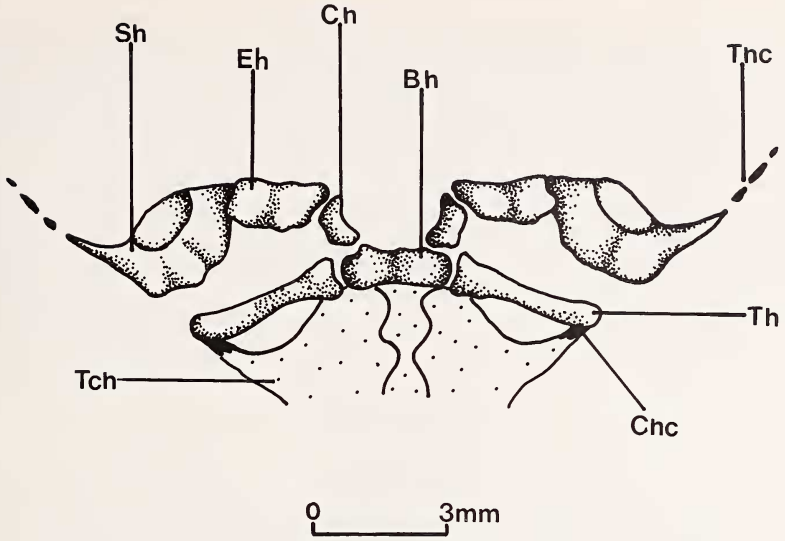

Fig. 2. Hyoid apparatus (ventral view) of *Chrysochloris asiatica*. Bh – basihyal; Ch – ceratohyal; Chc – chondrohyal cartilage; Eh – epihyal; Sh – stylohyal; Th – thyrohyal; Thc – tympanohyal cartilage

the position of attachment to the skull is slightly anterior to the stylomastoid foramen – a condition Howes (1896) termed "protrematic" (but see Sprague 1944 for problems associated with this definition) – and is marked by a tympanophyal pit in *Chrysospalax* (Forster Cooper 1928), and a canal (vagina processus hyoidei) in *Chrysochloris* and *Amblysomus*. The proximal, rostral aspect of the stylohyal contains a large, smooth surface that articulates in situ with the conspicuously broadened and flattened, ventral edge of the angular process on the dentary (Fig. 1). (When hyoid apparati are not available for direct examination, the distinctive, flattened base of the angular process serves as a convenient indicator of hyoid-dentary articulation.) In *Chrysospalax trevelyani,* the articular surface on the stylohyal bone is distinctly concave, and is displaced ventrally relative to all other species examined.

From our dissection, the stylohyal-dentary articulation appears to be a synovial "plane joint" (Hildebrand 1974) that permits independent movement of the mandible and hyoids during the devouring of prey (i.e. as the jaw is opened and closed, and the tongue is protruded and retracted). Associated with this joint are muscles that, inter alia, run from the rostral margins of the stylohyal articular surface to the caudolateral aspects of the dentary, and which seemingly act to tense the hyoid-dentary link, and constrain movement along a dorsoventral plane. The precise action of these muscles is currently under study.

While the hyoid apparati of only nine species were available for direct study, hyoid-mandible joints in all of the (13) chrysochlorid species (representing six genera) currently preserved in the Transvaal Museum were inferred from the presence of conspicuously flattened articular surfaces on the dentaries of preserved specimens. (Only *Cryptochloris* was not available.) No similar articular surfaces were found on the dentaries of rodent mole (Bathyergidae) or tenrec *(Tenrec eucaudatus)* specimens examined, nor have they been described in the literature on other mammals. Hyoid-dentary articulation may therefore be an unique, and characteristic, feature of all chrysochlorids.

Until the interaction of hyoid-associated muscles has been established, function(s) of the hyoid-dentary articulation in golden moles can be only suggested. A role in jaw

suspension, (similar to that played by the epihyal-mandible link of some fishes) can be excluded, since the hyoid-cranial attachment is too tenuous to supplement suspension of the mandible provided by the squamosal-mandibular hinge. A function in the detection and transmission of underground vibrations to the middle ear, similar to the prey-detection mechanisms of some primitive amphibians (see Hildebrand 1974), is also highly unlikely in view of the slender, cartilagenous hyoid-cranial link.

The most likely function of the enlarged hyoid bones and articulation is to enhance support for, and manipulatory ability of, the tongue. During the handling of natural, often writhing, prey (such as earthworms) chrysochlorids sometimes use their foreclaws to press the prey item to the ground, but for the most part rely on agile movements of the tongue, jaws and head. While the tongues of chrysochlorids are not particularly long (Sonntag 1923), they are very muscular, and are well supplied with keratinized and scoop-shaped papillae (Dobson 1882). During mastication, only orthal movement of the mandible is allowed by the tight squamosal-mandibular joint (Parsons 1901), and the zalambdodont cheekteeth serve mainly for the embrasure shearing of food, with little crushing thereof. Pieces of food apparently are then further homogenized between the horny surface of the tongue and the robust palatal ridges, before swallowing. This process involves forceful movement of the muscular tongue, so that a strong base for its support is imperative. The hyoid-cranial link seems too tenuous to provide sufficient support by itself. The hyoid apparatus and articulation, however, are sufficiently robust to provide additional support and suspension for the tongue, whilst also permitting its movement independently of the mandible.

This explanation assumes that hyoid-dentary articulation in golden moles is functionally related to their zalambdodont dentition. The apparent absence of hyoid-dentary joints in other taxa exhibiting zalambdodonty (such as tenrecs and selenodonts), however, suggests that this is only partly true: some other factor unique to the chrysochlorid lifestyle must also have been involved in the development of hyoid-dentary articulation. It is possible that accomodation of the well-developed neck musculature (which powers forceful upthrusts of the head during their unique style of burrow construction; Puttick and Jarvis 1977) may have necessitated a decrease in the size of the chewing muscles (the masseters are relatively small; Dobson 1882), with a concurrent, compensatory shift of emphasis from chewing movement of the jaws to increased masticatory action of the tongue during feeding.

Mammalian hyoid apparati show great morphological plasticity in relation to function (Sprague 1944), and due to their position, are very susceptible to environmental influences (Gasc 1967). For this reason, characters of the hyoid region are generally considered to have little phylogenetic value (Grasse 1955). While the phylogenetic significance of the unusual hyoid structure and topography in golden moles cannot be fully assessed until its functions are demonstrated, the uniqueness of hyoid-dentary articulation adds to the wealth of other anatomical information (Broom 1915; Butler 1972; Bugge 1974; Dobson 1882; Forster Cooper 1928; Roux 1947) indicating that chrysochlorids are extremely specialized mammals which should perhaps be afforded at least subordinal rank within the Insectivora.

Acknowledgements

We thank Dr. I. L. Rautenbach for funding and encouragement; Dr. N. van der Merwe for enthusiastic cooperation; Prof. J. Jarvis for specimens; Prof. M. Smuts and Prof. de Boom for useful discussions; Prof. J. Meester for useful criticism; Mr. A. Herholdt and Mr. W. Haacke, for assisting with translation; the Board and Director of The Transvaal Museum, and the Department of Anatomy, Faculty of Veterinary Science, of the University of Pretoria, for access to facilities. Funding from the Council for Scientific and Industrial Research via Dr. Rautenbach is gratefully acknowledged.

Zusammenfassung

Hyoid-dental-Gelenkungen bei Goldmullen (Mammalia: Insectivora; Chrysochloridae)

Auffällige Gelenkverbindungen zwischen dem Stylohyale des vergrößerten Zungenbeinapparates und den Dentalia des Unterkiefers sind beim Hottentotten-Goldmull, *Amblysomus hottentotus*, festgestellt worden. Bei weiteren Untersuchungen wurde bei allen Gattungen der Chrysochloridae außer *Cryptochloris*, der nicht zur Untersuchung zur Verfügung stand, auf dem Unterteil der Dentalia eine bemerkenswerte Gelenkfläche gefunden. Kontakt, in situ, zwischen dem Stylohyale und der Unterseite der Dentalia ist durch Sezierung *(A. hottentotus, Chrysochloris asiatica),* Röntgenuntersuchung *(A. hottentotus, Chrysospalax trevelyani, C. asiatica, Eremitalpa granti)* und Untersuchungen von aufgehellten, doppelgefärbten, unversehrten Exemplaren von *C. asiatica* bestätigt. Über derartige Gelenkungen ist bisher weder bei Goldmullen noch anderen Säugetieren berichtet worden. Wir kommen daher zu dem Schluß, daß es ein typisches Merkmal der Chrysochloriden ist, mit möglicher systematischer Bedeutung. Wahrscheinlich ist die Funktion eine stärkere Unterstützung der Zunge, die beim Kauen beteiligt ist. Gründliche weitere Untersuchungen der beteiligten Muskulatur könnten die taxonomische, systematische und funktionelle Bedeutung dieses eigenartigen Merkmals der Goldmulle weiter erläutern.

References

Broom, R. (1915): On the organ of Jacobson and its relations in the "Insectivora" – Part II. Proc. zool. Soc. Lond. **25**, 347–354.

— (1916): On the structure of the skull in *Chrysochloris*. Proc. zool. Soc. Lond. **32**, 450–459.

Bugge, J. (1974): The cephalic arterial system in Insectivores, Primates, Rodents and Lagomorphs, with special reference to their systematic classification. Acta anat. Suppl. **62**, 1–147.

Butler, P. M. (1956): The skull of *Ictops* and the classification of the Insectivora. Proc. zool. Soc. Lond. **126**, 453–481.

— (1972): The problem of insectivore classification. In: Studies in vertebrate evolution. Ed. by K. Joysey and T. Kemp. Edinburgh: Oliver and Boyd. Pp. 253–265.

de Beer, G. R. (1937): The development of the vertebrate skull. Oxford: Clarendon Press. Pp. 1–552.

Dobson, G. E. (1882): A monograph of the Insectivora, systematic and anatomical. Part 1. London: John van Voorst. Pp. 1–172.

Forster Cooper, C. (1928): On the ear region of certain of the Chrysochloridae. Phil. Trans. R. Soc., Ser. B. **216**, 265–283.

Gasc, J.-P. (1967): Squelette hyobranchial. In: Traite de zoologie: anatomie, systematique, biologie. Tome XVI Mammiferes: teguments squelette. Ed. by P. Grasse. Paris: Masson et Cie. Pp. 550–583.

Grasse, P. (1955): Anatomie et reproduction (Ordre des insectivores). In: Traite de Zoologie: anatomie, systematique, biologie. Tome XVII Mammiferes. Les orders: anatomie, ethologie, systematique. Ed. by P. Grasse. Paris: Masson et Cie. Pp. 1574–1641.

Hildebrand, M. (1974): Analysis of vertebrate structure. New York, Chichester, Brisbane and Toronto: John Wiley and Sons. Pp. 1–710.

Howes, G. B. (1896): On the mammalian hyoid, with especial reference to *Lepus, Hyrax* and *Choloepus*. J. Anat. Physiol. Lond. **30**, 513–526.

Kuyper, M. A. (1985): The ecology of the golden mole *Amblysomus hottentotus*. Mam. Rev. **15**, 3–11.

Meester, J. A. J. (1974): Family Chrysochloridae. In: The mammals of Africa: an identification manual. Ed. by J. Meester and H. W. Setzer. Washington: Smithson. Inst. Press. Pp. 1–7.

Meester, J. A. J.; Rautenbach, I. L.; Dippenaar, N. J.; Baker, C. M. (1986): Classification of Southern African mammals. Transv. Mus. Monogr. **5**, 1–359.

Nevo, E. (1979): Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. **10**, 269–308.

Parsons, F. G. (1901): On the muscles and joints of the giant golden mole *(Chrysochloris trevelyani)*. J. Anat. Physiol. Lond. **34**, 26–34.

Puttick, G. M.; Jarvis, J. (1977): The functional anatomy of the neck and forelimbs of the Cape golden mole, *Chrysochloris asiatica* (Lipotyphla: Chrysochloridae). Zool. Afr. **12**, 445–458.

Roux, G. H. (1947): The cranial development of certain Ethiopian "insectivores" and its bearing on the mutual affinities of the group. Acta zool. Stockh. **28**, 165–397.

Sonntag, C. F. (1923): The comparative anatomy of the tongues of the Mammalia. IX. Edentata, Dermoptera, and Insectivora. Proc. zool. Soc. Lond. **34**, 515–529.

Sprague, J. M. (1944): The hyoid region in the Insectivora. Am. J. Anat. **74**, 175–216.

Authors' addresses: G. N. Bronner, Elizabeth Jones, Transvaal Museum, P.O. Box 413, Pretoria 0001, South Africa; D. Coetzer, Department of Anatomy, Faculty of Veterinary Science, University of Pretoria, P.O. Box 12580, Onderstepoort 0110, South Africa